Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

Vol. 42 No. 8

BULLETIN

OF THE

TORREY BOTANICAL CLUB

AUGUST, 1915

The origin of dwarf plants as shown in a sport of Hibiscus oculiroseus

A. B. Stout

(WITH PLATES 26 AND 27)

The publication in 1901–1903 of Die Mutationstheorie aroused a new interest in the well-known sports or spontaneous variations of earlier writers. While Darwin had recognized the occurrence of such variations he did not consider that they were the sole means or even the most frequent means by which species originated. De Vries sought to separate mutability as a type of sporadic variability from fluctuating variability, to define quite different laws for the two, and to ascribe to the former the only power to give rise to forms of specific rank.

Since 1901 much further evidence has accumulated regarding the appearance, the behavior, and the heredity of so-called mutations. It is fully established that marked variations do appear and that these are often hereditary. This phase of the general doctrine of variation is fully established. Of the various practical and theoretical considerations presented by these cases none are more fundamental than those relating to the expression and the heredity of "newly born" characteristics.

The general conception of mutation and the categories of behavior that indicate the process were combined by De Vries with the doctrine that plant characters are to be considered as so exactly represented by definite hereditary units that they can be properly called "unit characters." De Vries especially em-

[The BULLETIN for July (42: 365–428. *pl. 21–25*) was issued July 29, 1915.]

phasizes this view in the preface of the English translation of Die Mutationstheorie (1909).

It has also been shown that numerous cases of hybridization result in an increased variability in the F_2 generation over that of the parents, in the production of intermediate forms, and in unexpected ratios. The Mendelian factorial hypothesis, which attempts to explain such phenomena, assumes that the difficulties of analysis in terms of unit characters indicate that characters are themselves the results of the combined action or interaction of hereditary units called factors to which various values can be attributed as seems necessary. There are some striking cases of reversion resulting from crosses that seem to support this view; as, for example, the production in sweet peas of the reversionary purple bicolor known as "Purple Invincible" from crosses between certain white flowering strains of "Emily Henderson" (Bateson, 1913, Chap. V). The developments of the Mendelian theory have led, however, to various and conflicting conceptions regarding the nature of the hereditary units and of the fundamental processes of mutation or discontinuous variation.

De Vries on the one hand considers that mutability is due to lability of hereditary physiological units; these change from stable to labile, from active to inactive (or latent) or even to a semilatent condition, giving irregularities of expression both in inbred and crossbred lines of progeny. Only in the rare cases of progressive mutation are new characters added and in none of the mutations is complete loss of hereditary qualities essential. The units of De Vries assume different degrees of activity; they are not uniform and consistent units in their influence.

In marked contrast to this view is the conception of Bateson that all variation is due to the presence or absence of "unit factors", that all true mutation is due to loss of factors, and that cases of discontinuous variation resulting from crosses are reversions which are due to recombination of factors. This view minimizes the occurrence of latency, ignores lability and insists on a rather rigid unity of assumed hereditary units, not in any sense comparparable with the appearance of the visible characters of plants.

These two very different interpretations indicate clearly the

difficulties that arise in the attempts to analyze the facts of heredity and variation in terms of units and raise anew the questions as to the validity of the conceptions regarding mutation.

It is the purpose of this paper to present the facts as thus far determined regarding the origin and the behavior of a marked variation in *Hibiscus oculiroseus* and to point out some considerations suggested by such cases.

THE DWARF FORM OF HIBISCUS OCULIROSEUS

The two plants shown in PLATE 26 are typical for the appearance of dwarf and robust plants of *H. oculiroseus* at the end of the first year of growth as handled in my cultures. Both plants were from seed planted in January, 1914. The seedlings were grown in pots in a greenhouse until May, when they were planted in adjoining beds in the experimental garden. The photograph was taken September 13, 1914. A glance at the plate will show the marked differences that exist between the two types. The dwarf plant is shorter, but is more branched with large well-developed lateral branches arising close to the base; the internodes are shorter, making the leaves more crowded; the leaves are smaller and many of them are somewhat irregular or asymmetrical in outline and many of them are crinkled. Few of the dwarf plants have thus far come into flower, but those that have showed flowers nearly if not fully as large as the robust types.

From the data regarding the ancestry of the dwarf plants, it appears that a plant of *Hibiscus oculiroseus* was obtained by the New York Botanical Garden from the firm of Pitcher and Manda in the year 1896. This firm obtained their original stock of this plant from Mr. W. F. Bassett of Hammonton, New Jersey, who introduced the plant (Britton, 1903) into the trade some years before. Bassett obtained the first plant of this type about the year 1880 from a colony of wild plants growing near Absecen, New Jersey. The plant was propagated by seed, and introduced into the trade. It was commonly called the "Crimson Eye."

Britton (1903) points out that this type differs from *H. Moscheutos* in several characters. *H. Moscheutos* in its most abundant form, at least in the vicinity of New York City, has flowers of a

rose color, lighter along the veins and becoming nearly pure white for about 1 cm. at the base of the corolla lobes. *Hibiscus oculiroseus* has a rose red or Tyrian rose eye about 2 cm. in radius, beyond which the petal is a sea-foam yellow. The flower pods are ovoid with a long tapering point, the calyx segments are triangular-lanceolate and nearly twice as long as broad. *Hibiscus Moscheutos* has a nearly globular bluntly pointed pod. On this account he gives the type specific rank under the name *H. oculiroseus*.

CULTURES OF H. OCULIROSEUS AT THE NEW YORK BOTANICAL GARDEN

Open-fed seed was collected from the plant obtained from Pitcher and Manda and planted for the purpose of increasing the stock of the species. The progeny (Nash, 1909) was composed in part of plants conforming to *H. oculiroseus* and in part of plants whose flowers suggested that the plants were hybrids between *H. oculiroseus* and the rose-flowered type of *H. Moscheutos*, an assumption which the writer has since proved to be true by controlled crosses.

At the time the writer began his investigations with *Hibiscus* (1911) there were seven plants of the *H. oculiroseus* characters growing in the Garden, all derived from the one parent plant. All of these were vigorous plants about five feet tall. Five of these plants have been used as parents and will be referred to as *O* No. 1, *O* No. 2, etc.

One of these plants (*O* No. 1) produces each year a considerable number of leaves, somewhat crinkled and irregular, and the uppermost internodes of the branches are somewhat shortened. One would be inclined to attribute this to a fluctuating variation due perhaps to local soil conditions. The other four plants show no trace of any of the dwarf characteristics.

PLANTS OF THE FIRST PEDIGREED GENERATION

In 1912, fifteen plants (Series I) were grown from open-fed seed collected from the plant *O* No. 1. Fourteen of these were robust and vigorous in growth, but three of them had some leaves

irregular in shape and also exhibited a shortening of internodes at the tips of stems quite identical to that of the parent plant and were in general intermediates between the robust type and the extreme dwarf type. One plant was of the dwarf type quite identical with the one above described. Ten of the plants, including the dwarf and one of the intermediates, were grown in 1913, when all bloomed. The dwarf plant (No. 1 of Series I) continued small and much branched with many crumpled leaves. Two capsules of selfed seed were obtained from this plant and one capsule was obtained from a sister plant (No. 5 of Series I) of the robust type.

As to flower coloration and pod character, nine of the ten plants were typical *H. oculiroseus*. One plant had flowers with faint pink coloration outside the eye in the blade of the corolla, although at a short distance or upon casual survey the flowers appeared to be typical *H. oculiroseus*. There was outside of this one plant no indication but what the seed obtained was strictly selfed, and even in this one case the flowers borne were not such as have been obtained in the F_1 hybrids between the parent plant and the only other type of *Hibiscus* growing in the vicinity of the seed parent.

The winter of 1913–14 was unusually severe on the *Hibiscus* plants growing in the experimental plots, killing about 1,500 plants of various cultures, including the dwarf plant (No. 1) and the robust plant (No. 5) of Series I, from which selfed seed had been obtained.

In addition to the plants of Series I, there were also grown during the summer of 1913 forty-five plants (Series VI) derived from selfed seed obtained during the summer of 1912 from the same parent plant (*O* No. 1). All of these were dwarf plants. Four produced flowers that were typical *H. oculiroseus*. No seed ripened and all the plants died during the winter of 1913–14. All the plants of this series were dwarfs, while of the fifteen plants of another series (Series I) from a pod of the same parent only one dwarf appeared as already noted.

The dwarf character of these plants was most conspicuous in comparison with the selfed progenies of four other plants of *Hibiscus oculiroseus* (sister plants of *O* No. 1) grown during the

summer of 1913 from seed of 1912. The data for these can be briefly summarized as follows: from plant *O* No. 2, nine plants were grown, of which four bloomed; from plant *O* No. 3, forty plants, of which ten bloomed; and from *O* No. 5, twenty-seven plants, of which none came into flower. All of the plants in these four series, 103 in number, were typical for the robust type with no trace of any of the dwarf characteristics. The twenty-four plants that bloomed were true to the *H. oculiroseus* type of flower. None of the plants matured seed and every one was killed during the winter of 1913-14.

PLANTS OF THE SECOND GENERATION

In the summer of 1914 three series of plants were grown, constituting a second generation in descent from the parent *O* No. 1. These may now be described.

Series VII. The parent of this series was a dwarf plant (No. 1 of Series I). Thirty-five plants were grown from seed of a single pod. Twenty-seven were uniformly of the dwarf type; one was a typical robust plant and seven were intermediates showing in slight degree the characteristics of the dwarf type. Six plants bloomed; one had eyed flowers with pale pink in the blade (quite similar to No. 8 of Series I), three had the eye somewhat diluted, and on two the eye of the flower was so diluted that the flowers appeared to be nearly pure white. The one plant of robust habit had flowers of a type which suggests that it is a stray plant of hybrid origin.

Series VIII. Of the same parentage as the Series VII. Forty-six plants were grown from selfed seed of a single capsule. Forty-five of these were dwarf quite like the one from this series shown on PLATE 26. One plant was intermediate but was different from other intermediates in possessing a considerable development of lateral branches, the main branch was itself robust and the leaves were only slightly crinkled. The five plants that bloomed were all typical for the *H. oculiroseus* type and were only slightly if any smaller than the flowers of robust plants. The plants of this series are shown in the middle of PLATE 27 with the marker standing in their midst. The plants of Series VII are shown

beyond the label stake in the rear. The intermediate plant in Series VIII just mentioned is shown at point *a*. To the right in the foreground are hybrids between *O* No. 2 and a plant of *Hibiscus Moscheutos*, and to the left are hybrids between two types of *H. Moscheutos*, all of the same age as the dwarf plants.

Series IX. The thirty-four plants of this series were grown from the selfed seed of one capsule of plant No. 5 of Series I. The parent was a robust plant. Thirty-three of the plants were of the robust type quite uniformly like the one of this series shown on PLATE 26. One plant was classed as an intermediate; it was smaller than the others, its leaves were somewhat crinkled, but it was not branched from the base. Twelve plants produced flowers; ten of these were typical *H. oculiroseus*, one had flowers with slight pink coloration outside the eye, and on one plant the flowers were quite pink outside the eye, quite like the flowers produced by hybrids between *H. oculiroseus* and the pink-flower type of *H. Moscheutos*.

Nearly all the plants of these three Series (VII, VIII and IX) lived through the winter of 1914–15 and were grown during the summer of 1915 in the same beds as in the previous year. In the second year of growth several main stems, usually three to five, are produced by the single cluster of roots belonging to a plant. As the plants were grown about 30 cm. apart they were much crowded in the second year, which is a condition that does not favor the development of secondary branches and hence the plants were much less bushy than in the first year of growth. Under these conditions there were fewer differences between plants previously classed as intermediate and dwarf.

In 1915 the plants of Series VII ranged from 1.25 m. to 1.6 m. in height with the exception of the plant classed as robust which was 2.08 m. tall but which from the character of its flowers appears to be an accidental hybrid. Series VIII ranged from 1.3 m. to 1.6 m. in height. The dwarf plant shown to the left in PLATE 26 had four main branches and stood 1.45 m. tall and was typical for the average plant; the plant shown at point *a* in PLATE 27, classed as intermediate in 1914, was of nearly the same height and appearance. Series IX, described as robust in 1914, varied

from 1.75 m. to 2 m. in height with the average quite 0.3 m. taller than that of Series VII and VIII.

During 1915 there was also grown from seed a series of twenty-eight plants from selfed seed of plant *O* No. 1, the parent of the Series I and VI. On August 25, these plants varied from 0.4 m. to 0.75 m. tall and nearly all had the dwarf characteristics. The series showed greater variation in general vigor than did the plants of Series VII and VIII in their first year of growth. A series of twenty-three plants derived from selfed seed of one of the robust plants of Series I, grown at the same time were in comparison decidedly robust averaging from 0.8 m. to 1 m. in height and with no crumpled leaves or strongly developed lateral branches. Another series of eleven plants descended from a plant of Series I classed as intermediate was on the whole intermediate between the two series just mentioned.

SUMMARY OF THE CULTURES

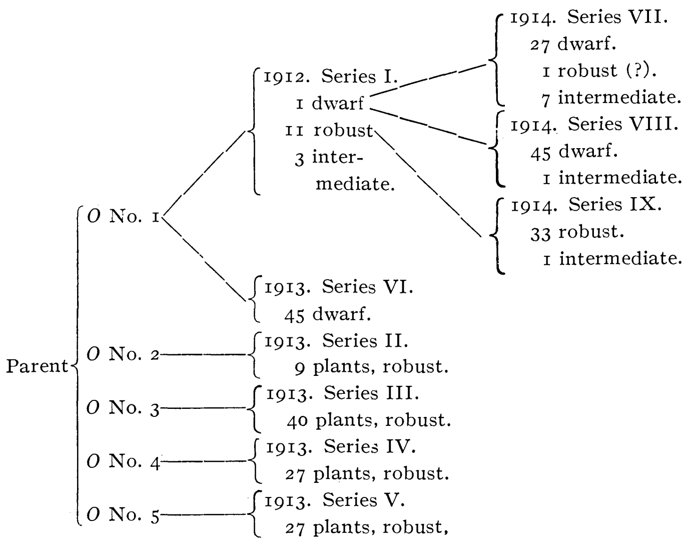
A total of 288 plants have been grown (at least through a single season) from seed obtained from five sister plants of *Hibiscus oculiroseus*. The dwarf type of plant has appeared only among the progeny of a single plant (*O* No. 1); the 103 plants derived from the other four sister plants were without exception of the robust type.

There was much diversity among the progeny of the plant *O* No. 1, and the two series of plants grown in the first generation gave quite different proportions. In Series I, there were eleven robust, three intermediate and one dwarf; in Series VI there were forty-five plants, all of which were dwarf.

The progeny of a single dwarf plant (the only one that has thus far matured seed) was composed of one robust (later appearing to be an accidental hybrid), eight intermediate and seventy-two dwarf plants. While the dwarf type has not bred true the greater number of the progeny are of that type. There is a pronounced tendency to breed true. Robust plants in this line of descent do not always breed true, as the only one tested gave one intermediate plant and thirty-three robust plants.

A condensed schematic presentation of these facts regarding

the progenies of different lines of descent, not including the series started from seed in 1915, is given in the accompanying diagram.



DISCUSSION

The dwarf type of *Hibiscus oculiroseus* constitutes a marked and distinct variation from the usual robust type of the species. It has smaller leaves, many of the leaves are crumpled, the internodes are shorter, and there is an increased development of branches. It is such group-differences as these that constitute the elementary species of De Vries, for, as he states (1901, p. 176): "Elementare Arten unterscheiden sich von ihren nächsten Verwandten mehr oder weniger in allen ihren Merkmalen." All the changes, however, are considered to be a result of a change in the condition of a single pangen.

It is difficult or impossible to describe such a mutation in terms of definite characters that have been gained or lost. The ordinary type of development of the leaves and internodes have been modified mainly in the direction of arrested growth, while the amount of branching has been increased, due chiefly to the development of basal lateral buds that usually remain dormant.

In comparison with the robust type the characteristics of the typical dwarfs are readily recognized, the general effect being

quite adequately shown in the illustrations on PLATES 26 and 27. The characteristics of the two types can be listed as follows:

Robust form	*Dwarf form*
First year of growth, 0.8–1.1 m.	0.4–0.75 m.
Second year of growth, 1.75–2 m.	1.25–1.6 m.
No branching from base of shoots.	Large branches from base.
Internodes about 30 in number.	Internodes about 30 in number, but all proportionally shorter.
Leaves ovate, larger ones lobed, palmately veined, densely white stellate-pubescent beneath, glabrous above; leaves all flat.	Leaves identical except that the largest are smaller than the average of robust type; many leaves crinkled.
Flowers and fruit are typical *H. oculiroseus.*	Flowers and fruit identical with those of robust form; apparently no smaller.

While typical plants classed as robust and dwarf were very uniform in the above characteristics, there were a few plants, as noted, described as intermediates or semi-dwarfs, which possessed in some degree of development one or more of the characters of the dwarf form but which in the second year of growth were less distinguishable.

The mutant of *Oenothera Lamarckiana* that most nearly approaches in its characters the dwarf *Hibiscus* is, of course, *Oe. nanella.* The principal characteristics of this plant compared with those of the parent form as given by the description of De Vries may be given as follows:

Oe. Lamarckiana	*Oe. nanella*
Robust: 1.5–1.8 m. tall.	Dwarf: about one-fourth as tall as *O. Lamarckiana*, often blooming when 10–20 cm. tall.
Secondary branches abundant and strong.	Secondary branches lacking or nearly absent.
	Internodes much shorter making leaves and flowers more compact.
Leaves ovate-lanceolate; long petioled, much crumpled surfaces.	Leaves sessile or nearly so; broad at base, often auriculate or heart-shaped; petioles very brittle.
Flowers with petals 3–4 cm. long; buds thin, tapering to a point.	Flowers very nearly as large; buds often laterally twisted.
Fruit and seeds normal.	Fruit and seeds of almost normal size.

The dwarf *Oe. nanella* differs from *Oe. Lamarckiana* in nearly all of its vegetative organs. De Vries maintains, however, that such a mutation is brought about by a change in the activity of

a single hereditary "pangen," but that the visible result depends only partly on the direct results of the changed condition in one pangen. On this point he states (1901, p. 305): "Der äussere, sichtbare Erfolg hängt also nur zum Theil von der Mutation, zum Theil aber auch von den älteren Merkmalen ab. Oder mit anderen Worten, die neue Art kennzeichnet sich in der Regel nicht durch eine enizige neue Eigenschaft, sondern dadurch, dass veile oder alle Organe in bestimmter Weise umgestaltet wurden." This means that in the case of *Oe. nanella* when the *alta* pangen (1913) becomes inactive it affects not only the height of the plant but also produces a transformation of many other characters, such as the nature of the leaves and the branching. De Vries states regarding *Oe. nanella* (1904, p. 532): "The most remarkable feature is the shape of the leaves. They are broader and shorter, and especially at the base they are broadened in such a way as to become apparently sessile. The stalk is very brittle, and any rough treatment may cause the leaves to break off." These remarkable differences in the leaves are brought about, De Vries assumes, by a change in the "*alta* pangen", a pangen concerned with the height of the plant. Such a view is, it would appear, *directly opposed to a conception of independence between heredity units*. We get in such cases the clearest possible conception of the application of De Vries's idea of a heredity unit ("pangen") as an element of the germ-plasm which affects and determines the character of a plant as a whole, constitutionally, and in all or many of its characters. Such a view is quite different from the units of Weismann, which were assumed to be individual in effect and sufficiently numerous to correspond directly to every detailed feature of expression.

The original Mendelian doctrines of unit characters assumed qualitative germ cell units, independent in action, and each responsible for the expression of a character. Color and wrinkledness of peas (qualities of the cotyledons) were considered as separable hereditary units quite independent of any preformation of the cotyledons themselves. Mendelian theories have been concerned with the phase of development and heredity which involves qualities, and though evading the difficulties of assumed spacial relationship in preformation, they assume that the qualitative

values of the "factors" are predetermined. It is an important fact established especially by Mendelian studies that qualities of organs may appear and disappear independently of the organ and to certain degrees independently of each other. This suggests that the older conceptions of the preformation of organs as such do not hold and that a hereditary unit for an organ with all its characteristics does not exist. This is very clearly seen in the numerous studies of inheritance and variation of color in which organs like petals, leaves, and stems of plants, eyes of insects, etc., re nain quite the same except for color. Such facts emphasize on the one hand the wide possibilities of latency as most excellently developed by De Vries, and on the other the most evident fact that qualities which appear to be localized in organs are more often general qualities of the entire organism, the development of which is a matter of intercellular and inter-tissue relationships.

The arguments of De Vries consistently seek to establish the doctrine of the fewness of the pangens. On this basis dwarfness is assumed to be the same in all the different cases in which it appears throughout the plant kingdom.

No consistent uniformity, however, exists among the dwarf types derived in different species or even in the same species. Some types of dwarf garden peas appear to differ from tall varieties chiefly in the character of the internodes. In the "brachytic" varieties of cotton (Cook, 1915) the shortened internodes a ıd modified leaves and bracts are usuall confined to the fruiting branches. Numerous types of dwarf and semi-dwarf types exist in many species, a notable instance of which has been recently described by Bartlett (1915), who found that two dwarf types arose in a single pedigreed generation of *Oenothera Reynoldsii*. One of these, *semialta*, is about half as tall as f. *typica* and has a very dense and showy inflorescence, in which the fruits and flowers are very little smaller than in the parent form. The leaves, however, are decidedly reduced. As described by Bartlett (1915, p. 130) the sister dwarf "*debilis* is more variable in size than mut. *semialta*, but averages about half as high as the latter. Its fruits and flowers are somewhat reduced, but by no means proportionally to the plant. The leaves, on the contrary, are much more reduced than those of mut. *semialta*".

Bartlett has not discussed these in terms of characters that have been gained, lost, or modified, but does point out that the appearance of these two dwarf forms as sister mutants in the rather large number of individuals "bears a certain degree of resemblance to Mendelian segregation." The case is especially interesting in affording a record of the simultaneous origin of hereditary variations from a single parentage giving dwarf forms of markedly different characteristics.

Furthermore, the facts of variation resulting from hybridization involving dwarf forms indicate a diversity of behavior quite in line with the above-mentioned facts. Mendel considered that the dwarf garden pea differed from the tall in a single character pair and that he obtained neither intermediates nor a greater range of variation in the F_2 generation. Darbishire (1911) considers that this is the case and that the dwarf garden pea differs from the tall variety only in respect to two types of internodes, long and short. Punnett (1911, p. 35) applying the conception of presence and absence very generally to peas states "all peas are dwarf, the tall pea is a dwarf plus a unit factor." This generalization is not borne out by the data. Lock (1904) in progeny of crosses between a tall and a semi-dwarf ("Satisfaction" and native No. 2) found in the F_2 great variation in habit ranging from very robust to very feeble dwarf. Although he considers that there must be some sort of Mendelian segregation if the internodes are solely considered, he admits that "this cross seems to afford an example of remarkable intensification of both the allelomorphic characters of the same pair, namely tallness and dwarfness, the former in the F_1 and both in the F_2 and later generations" (p. 414). Keeble and Pellew (1910) in crossing two well-known staple semi-dwarfs varieties of the garden pea obtained in the F_2 a wide variation, giving both dwarf and tall as well as intermediates. They conclude that length of internode and width of stem are both involved and in their interpretation dwarfs lack both factors, semi-dwarfs lack one and talls possess both. Height in sweet peas is also of complex character, as breeding studies of dwarf, semi-dwarf and tall varieties have shown. Crosses with bush and "Cupid" give an F_1 that is tall and an F_2 with variation involving plants that include tall, bush and

two types of "Cupid". Bateson attempts to explain this case as he does all cases of increased variation in terms of presence or absence of factors, giving *different interactions in different combinations.* The point is clear that greater variability does develop and that not only is height of sweet peas evidently a compound character, but that the assumed factors take on different values. For example, the factor T ("tallness") when combined with P (erect: branching) gives the bush variety. The two sets of allelomorphs assumed in this case are not independent units in expression. It may be emphasized that the original rigid unit-factor hypothesis is being given up in favor of the admission, as we see in this case, of a marked modifiability of the effect of the assumed factors. The integrity of the assumed units in these cases can only be maintained by assuming a permanence in them, which is entirely at variance with the visible results which they are assumed to produce.

The behavior of the dwarf characteristics of *Oenothera nanella* in hybridization is of special interest in this connection. The group of characters appearing in *Oe. nanella* go together in crosses with *Oe. Lamarckiana*, not as a unit giving alternative expression but in the splitting that develops in the F_1 generation giving the parent forms as twin hybrids. De Vries assumes (1913) that the *alta* pangen is inactive in *Oe. nanella* and labile in *Oe. Lamarckiana.* In this case inactive $\times$ labile gives both inactive and labile.

When *Oe. rubrinervis* is crossed with *Oe. nanella* splitting also occurs in the F_1 giving *Oe. Lamarckiana* and a new type called *Oe. subrobusta.* The *alta* pangen in *Oe. rubrinervis* is assumed to be active, so in this case active $\times$ inactive = labile and inactive + active. The *Oe. subrobusta* form splits in the next generation, giving dwarf forms which, however, are evidently not *Oe. nanella. None of the types derived are like either of the two parent forms.*

Again when *Oe. muricata* is crossed with *Oe. nanella* the F_1 is of two new types called *Oe. laeta* and *Oe. velutina.* *Oe. velutina* splits up in the F_2 giving a dwarf *Oe. murinella* that is not like *Oe. nanella.* None of the types are like the parent forms. The assumed condition of the *Oe. alta* pangen in this case is active $\times$ inactive = labile, active and inactive.

The appearance of twin hybrids not like the parents and of sec-

ond generation dwarfs not like *Oe. nanella* is also the rule in crosses between *Oe. nanella* and *Oe. Hookeri*, *Oe. Cockerelli*, *Oe. cruciata* and also *Oe. biennis* when the latter is the seed parent.

When *Oe. nanella* is fertilized by pollen from *Oe. biennis* the F_1 is composed largely of dwarf plants. In the earlier crosses De Vries reports a few tall plants and many dwarfs (1913, p. 241) but from a cross in 1907 he obtained only dwarfs which, however, he classed in two types, *Oe. semialta* and *Oe. debilis*, each of which was different from the *Oe. nanella* parent. In this case the condition of the *alta* pangen in the hybrids is assumed to be inactive × labile, which is the same condition assumed for *Oe. nanella* × *Oe. Lamarckiana*.

De Vries finds in such behavior evidence of the production of new species in groups by hybridization. He assumes that a few pangens are involved and that those exist in few conditions. The integrity of such units can only be assumed by calling in such all-sufficient properties as lability and inactivity which admit of very sporadic behavior.

It is generally assumed that a new elementary species arises suddenly without transitional forms. This is not the case with the dwarf type of *Hibiscus* here described. The plant *O* No. 1 from which all dwarf plants thus far obtained have arisen, possessed a few of the characteristics of the dwarf. The next generation gave dwarf, intermediates and robust plants in quite irregular numbers in the two series grown. Bartlett (1915) describes two dwarf types arising in a progeny of *Oe. Reynoldsii*, one of which (*semialta*) is intermediate in general stature and has leaves less reduced than in the extreme dwarf form (*debilis*). Variations such as these are not like ordinary fluctuations in giving a frequency distribution agreeing with Quetelet's law and they do not conform to the Mendelian ratios of segregation, although as Bartlett points out, there is much in the behavior that suggests the segregation assumed by Mendelian interpretation. *They are irregular and sporadic variations* involving different degrees and intensity of change. The most marked of these involve changes affecting the character of several organs.

Further evidence regarding irregular expression of characters is

seen in the well-known cases cited by De Vries of non-isolable races, eversporting varieties, and inconstant species, indicative of irregular and sporadic inheritance and expression of ever present tendencies which in these cases rigid selection fails to isolate.

That there are cases of variation that are cumulative is evident. De Vries especially has given data on two such cases. In a race of *Chrysanthemum segetum*, having an average of twenty-one ray florets in the terminal inflorescence in a crop of 1,500 plants one plant was found with four lateral flower heads with twenty-two ray florets. Seed from this plant gave a progeny of 423 plants one of which had a terminal inflorescence of thirty-four rays. Seed from this plant gave a mixed progeny with one plant having sixty-six ligulate florets, three of which were among the tubular disk flowers. Seed from this plant gave progeny with florets ranging from thirty-three to one hundred and one with a few completely double flowers.

In respect to these results De Vries says (1901, p. 526): "Es wird sich jedem Leser die Frage aufdrängen: ist dieser Uebergang ein allmählicher oder ein stossweiser gewesen? Mir scheint das letztere der Fall zu sein, aber es hängt dabei viel ab von der Bedeutung, welche man den Wörtern giebt. Jedenfalls geschah die Umwandlung nicht im Laufe der Jahrhunderte, wie es die Selectionstheorie anzunehmen pflegt, nicht einmal brauchte es dazu Jahrzehnte. Drei Jahre genügten, und solches in einer Cultur von nur wenigen Quadratmetern Umfang."

De Vries considers that this result is due to the reappearance of a latent character. It is not clear what the latent character is in this case. The species already possessed ray flowers in the outer circle of flowers. The development of a so-called double-flowered race consisted of a change of tubular flowers to ray flowers. Furthermore, as wholly double flowered plants are sterile, the double flowered plants are obtained continually by planting seed from plants not fully double flowered.

A similar case is seen in the development of *Linaria vulgaris peloria*. Individuals of certain races produce rarely a single peloric flower, an evidence De Vries considers of a semi-latent character which seldom becomes active. Seed from two such plants gave

out of a generation of two thousand one hundred plants, twenty plants having only peloric flowers. Progeny of these peloric plants gave ninety per cent. true to the type. In both *Chrysanthemum segetum* and *Linaria vulgaris peloria* self sterility made it difficult to grow pure line progenies. De Vries points out (1901, p. 564) that while he considers these as cases of mutation they are of a type quite different from that in *Oenothera*. In regard to the origin of such variations that are hereditary the evidence is not at all conclusive that slight variations may not be inherited even in a cumulative manner.

That this is the case is further suggested by the difficulty of drawing a definite line of distinction between species, varieties and races. De Vries, who has written most fully on this point from the standpoint of genetics, states that the best examples of varieties are those showing latency of a single character which may be just as constant as species (1901, p. 119); again he treats *O. nanella* (1901, p. 256) as a variety simply because somewhat similar dwarf types recur in a great number of species. He also gives the general view that varieties usually differ in one character (1901, p. 363); he states in another connection that the chief difference between improved races and species, even the smallest of elementary species, is the instability of the former and the stability of the latter (1901, p. 84); but we may note that inconstant species do occur (1901, p. 270).

It is clear that some cases of sporadic variation reproduce more true to type than others. The so-called law of mutation that "neue elementare Arten sind meist völlig constant, vom ersten Augenblicke ihrer Entstehung an" (1900, p. 175) is itself a qualified statement. The difficulty of assigning a definite heredity in terms of unit characters or unit factors to "newly born" characteristics which appear in mutations has become apparent. This is especially recognized in part by the view of Gates that mutation is a phenomenon of variability which is quite distinct from heredity.

Thus far progeny has been grown from only one of the dwarf plants of *Hibiscus oculiroseus*. One capsule of seed gave forty-six plants, all but one of which were dwarf, and another capsule gave twenty-seven dwarf, one robust and seven intermediates as judged

by the growth made the first year. The type appears to be only slightly inconstant. Further breeding tests will determine if the type becomes more constant by selection and if differences exist between the progenies of different dwarf plants.

There has been much discussion recently regarding the possibility of the association of hybridization with mutation especially in the Oenotheras. The rather well-known history of *Hibiscus oculiroseus* and its dwarf mutant is of significance in this respect. The wild form of *H. oculiroseus* was originally found in a region in which the species *H. Moscheutos* exhibits much polymorphism, involving problems which the writer now has under investigation. Its affiliations with this species are so evident that for some time it was known as a variety. The several differentiating characters possessed by *H. oculiroseus* have already been noted and while a few variations have been observed in my pedigreed cultures the species breeds remarkably true to type. In fact the only variations that have appeared have been among the progeny of the plant giving dwarf plants, and none of the variations suggest that this particular plant is a hybrid at least of the usual type. As far as now known, *H. oculiroseus* has a limited distribution in nature and since it is closely associated with *H. Moscheutos* it may well be that it has been derived from this species.

Mr. George William Bassett, owner of the William F. Bassett nurseries, writes in 1915: "We have never, to my recollection, observed any dwarf tendency in *Hibiscus* 'Crimson Eye.' Nor have we had any occasion to throw any out for any cause." It does not appear that dwarf forms have appeared in the cultivation of the species. Mr. Norman Taylor reports to the writer that he has observed in Long Island colonies of dwarf plants of the pink-flowered form of *H. Moscheutos*.

The evidence indicates that the dwarf form is of spontaneous origin. There is no series of characteristics belonging to either *H. Moscheutos* or the parent stock of *H. oculiroseus* that can be considered as combining to produce the dwarf, an interpretation given to the origin of *Oe. gigas* by Heribert-Nilsson (1912). The immediate parent (*O* No. 1) of the dwarf plants possessed in slight degree the characteristics of crinkled leaves and shortened inter-

nodes which later appeared more intensified in the dwarf plants. This, coupled with the variability of the progeny, might be considered by Mendelians to indicate that the parent plant was a half-mutant. While it is no doubt true that such cases do occur (a most notable case is that of *Oe. semigigas*), it is evident that the conception has been applied to many cases of irregular inheritance and sporadic variation and even to instances of cumulative variation.

A most important type of discontinuous variation is that of simultaneous variation in a group of characters, well illustrated by the dwarf *Hibiscus*. Not only is a number of characters modified but the habit of profuse branching from the base appears as a character quite new to the parent species. Such phenomena are not well explained on any conception of continuous unit characters.

Bateson does not admit that such simultaneous variation can occur as a sporadic variation. He does not believe in the mutation and inheritance of group-characters as described by De Vries and already mentioned with respect to characters of *Oe. nanella*. He prefers to think of the phenomena as due to a recombination of factors. His strongest evidence for this view is the apparent marked reversions that appear in certain crosses. If, however, recombinations can give new groups or develop characteristics new to the particular race and species, his analysis is of doubtful validity.

To assume that a variation such as the dwarf *Hibiscus* is due to a single change in a single hereditary unit is to assign to the units different values and to admit of interaction between units. On the other hand to assume that there are hereditary factors that are themselves stable but that can interact upon each other in various ways is to assign different values to the supplementary or coördinating units and to the various interactions between them. This makes the comprehensive description of the processes of heredity in terms of units other than characters of doubtful validity.

It is quite clear that hereditary variations giving dwarf forms of various degrees of intensity and extensity do arise. If in all cases single characters, factors or other hereditary units are con-

cerned the evidence is clear that they possess different potencies and belong to quite different categories, or else that they undergo quite different sorts of changes not only in different species but in the same species, variety, strain or even pure line.

The accumulation of evidence from all lines of plant breeding shows that sporadic and irregular expression and inheritance of characters are frequent and are widely distributed among plants, and that ordinary stable characters and combinations become split up and modified in processes of both mutation and hybridization, giving variability not conforming to the usual laws of fluctuating variability.

SUMMARY

A dwarf form of *Hibiscus oculiroseus* has appeared in a pedigreed culture as a sporadic variation. It differs from the robust form in possessing a smaller stature, shorter internodes, smaller leaves, many crinkled leaves and in the development of lateral branches from the base of the main stem.

Plants intermediate between the dwarf and the robust forms appear. These possess one or more of the characters of the dwarf type in some degree of development.

All the dwarf plants thus far obtained are the progeny of a single plant (*O* No. 1). No dwarf plants appeared among the 103 plants grown as progeny of four sister plants of plant No. 1.

The parent plant of this dwarf (*O* No. 1) possessed already in slight degree the characteristics of crinkled leaves and shortened internodes.

The dwarf plants appeared in varying numbers along with robust and intermediate types. One series (Series No. I) was composed of one dwarf, eleven robust and three intermediate plants; another series (Series VI) was composed of forty-five dwarf plants.

There is a strong tendency for the dwarf form to breed true. In a total of eighty-one plants grown from seed of a dwarf there were seventy-two dwarf plants, eight classed as intermediates, and one that was robust (Series VII and VIII).

It is difficult to describe the dwarf type in terms of characters that have been lost or gained. The smaller and crinkled leaves and the shortened internodes are evidences of reduced or arrested

growth. In the marked development of branches from the base there is increased growth or at least development of buds that usually remain dormant.

There is no series of characters of either *H. oculiroseus* or *H. Moscheutos* that can be considered as combining in hybridization to give the dwarf.

The simultaneous appearance of variations involving modifications of groups of characters and of intermediates of various kinds exhibit sporadic variations of various degrees of intensity quite in line with the general evidence of the sporadic nature and wide range of such variations.

NEW YORK BOTANICAL GARDEN

BIBLIOGRAPHY

Bartlett, H. H.

1915. Mutation *en masse*. Am. Nat. **49**: 129–139.

Bateson, William.

1913. Mendel's Principles of Heredity. Third impression. Cambridge.

Britton, N. L.

1903. The rose mallows. Jour. N. Y. Bot. Garden **4**: 219–220.

Cook, O. F.

1915. Brachysm, a hereditary deformity of cotton and other plants. Jour. Agric. Research **3**: 387–400. *pl. 53–62.*

Darbishire, A. D.

1911. Breeding and the Mendelian discovery. London.

Heribert-Nilsson, N.

1912. Die Variabilität der *Oenothera Lamarckiana* und das Problem der Mutation. Zeitschrift für Ind. Abst. Vererb. **8**: 89–231.

Keeble, F., & Pellew, C.

1910. The mode of inheritance of stature and of time of flowering in peas (*Pisum sativum*). Jour. of Genetics **1**: 47–56.

Lock, R. H.

1904. Studies in plant breeding in the tropics. Ann. Roy. Bot. Gardens. Peradenya. **2**: 299–414.

Nash, G. V.

1909. The aquatic garden. Jour. N. Y. Bot. Garden **10**: 205–208.

Punnett, R. C.

1911. Mendelism. New York.

Vries, Hugo de.

1901. Die Mutationstheorie. Vol. I. Leipzig.

1904. Species and varieties. Their Origin by Mutation. Chicago.

1909. The mutation theory. Vol. I. Translation by Farmer (J. B.) and Darbishire (A. D.) Chicago.

1913. Gruppenweise Artbildung unter spezieller Berücksichtigung der Gattung *Oenothera*. Berlin.

Explanation of plates 26-27

PLATE 26.

To the left, typical plant of the dwarf form of *Hibiscus oculiroseus* (Plant No. 14 of Series VIII). To right typical plant of the robust form (Plant No. 23 of Series IX). Photograph taken September 13, 1914. Both plants are seven months old.

PLATE 27.

View in garden. In center with marker in the midst is a series (Series VIII) of dwarf plants. Plant indicated at *a* is an intermediate. At the right is a series of hybrids between *H. oculiroseus* (Plant *O* No. 2) and the pink-flowered type of *H. Moscheutos*. To the left is part of a series of hybrids between white-flowered and pink-flowered forms of *H. Moscheutos*. The three series are of the same age and illustrate the difference between the dwarf and the robust forms.

STOUT: HIBISCUS OCULIROSEUS

STOUT: HIBISCUS OCULIROSEUS